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Seasonal dynamics of growth and mortality suggest contrasting population structure and ecology for cod, pollack, and saithe in a Norwegian fjord

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We study the dynamics of Atlantic cod (*Gadus morhua* L.), pollack (*Pollachius pollachius* L.), and saithe (*Pollachius virens* L.) in Masfjorden, a small fjord in western Norway. Annually, cohorts of pollack and cod grow in size and decline in abundance, as expected of closed populations, whereas saithe virtually disappear before maturity. Seasonally, in contrast, the dynamics of cod and pollack differ. Pollack shows a regular growth pattern, with most of the growth taking place in summer. Its abundance-at-age shows strong seasonal variations, with a marked increase from spring to summer followed by a decline through autumn and winter. These patterns relate partly to seasonal changes in depth distribution and catchability. Combined with the observation that spawning-stage pollack are abundant in spring, we interpret these patterns to suggest that pollack in Masfjorden represent a dynamically independent unit. Seasonal changes in abundance are less marked for cod, and seasonal changes in depth distribution seem insignificant. However, cod shows an unusual pattern in length-at-age, with no apparent growth in summer and fast growth in autumn. These patterns suggest that the population structure of cod may be more open than that of pollack and may involve mixing of more than one population component.

Keywords: Gadidae, population ecology, seasonal dynamics, spatial population structure.

Introduction

Gadoids are important predators in temperate coastal ecosystems, and many gadoids are also important for both commercial and recreational coastal fisheries. Atlantic cod (*Gadus morhua* L.) in particular is a highly appreciated and valuable catch. Even for this high-profile species

(Kurlansky, 1997), the structuring of coastal cod resources remains insufficiently known (ICES, 2005; Nedreaas *et al.*, 2008). However, an increasing body of evidence from tagging and genetic markers suggests that, in many areas, coastal cod populations show fine-scale spatial population structure (Jakobsen, 1987; Knutsen *et al.*, 2003, 2011; Pampoulie *et al.*, 2006; Kovach *et al.*, 2010). Different population components may overlap in space and time, especially during the spawning time (Wennevik *et al.*, 2008; Kovach *et al.*, 2010; Grabowski *et al.*, 2011), making detection of population structure difficult. In general, presence of fine-scale population structure is relevant for fishery management because population components may differ in their life history and productivity (Ricker, 1958; Paulik *et al.*, 1973; Hilborn *et al.*, 2003), and cod is no exception (Smedbol and Stephenson, 2001; Hutchinson, 2008; Olsen *et al.*, 2008; Wright *et al.*, 2011).

Cod is among the primary targets in commercial and recreational coastal fisheries in Norway (Nakken, 1998; Nedreaas *et al.*, 2008; Vølstad *et al.*, 2011). Coastal cod resources are managed as three stocks: (i) Norwegian coastal cod north of 62°N, (ii) North Sea cod including coastal cod from 62°N southwards to Lindesnes near the southern tip of Norway (58°N 7°E), and (iii) coastal cod along the Skagerrak coast from Lindesnes eastwards to the Swedish border (Nedreaas *et al.*, 2008). Tagging and genetic studies indicate that, at least in some areas, these management units actually contain discrete population components showing consistent differences in migration patterns and genetic markers, with each fjord system hosting a local subpopulation of cod (Jakobsen, 1987; Knutsen *et al.*, 2003; Jorde *et al.*, 2007). Elsewhere, anecdotal evidence and tagging studies suggest that many fjords may host two distinct types of cod: (i) resident "fjord cod" that spend their whole life in the fjord, and (ii) migratory "bank cod" that enter the fjord for spawning only and that look different from the fjord cod (Jakobsen, 1987; Nedreaas *et al.*, 2008).

For gadoids other than cod, information on population structure and ecology is often extremely limited. For example, pollack (*Pollachius pollachius* L.) and saithe (*P. virens* L.) are important predators along the Norwegian coast (Giske *et al.*, 1991; Salvanes and Nordeide, 1993) and are commonly caught in recreational fisheries (Vølstad *et al.*, 2011), yet their population ecology and population structure remain poorly known. In the North Sea, pollack was analysed for the first time by ICES in 2011, noting that generally little is known about the species and that it was unclear whether there should be one or several management units (ICES, 2011a, b).

This study is based on sampling conducted during a cod stock enhancement experiment carried out in Masfjorden, a typical northern temperate fjord located in western Norway (Fosså *et al.*, 1994; Smedstad *et al.*, 1994; Svåsand *et al.*, 2000). In addition to monitoring of the cod stock in Masfjorden, sampling and modelling was carried out to understand and describe the ecosystem, the trophic interactions therein, and its potential for production of cod (Giske *et al.*, 1991; Salvanes *et al.*, 1992; Salvanes and Nordeide, 1993). The studies included investigations of other dominant gadoid species in the fjord than cod, particularly pollack, poor-cod (*Trisopterus minutus* L.), and saithe (e.g. Salvanes and Ulltang, 1992; Salvanes and Nordeide, 1993; Fosså *et al.*, 1994; Salvanes, 1995).

Here, we utilize the material from Masfjorden to study whether sampling carried out at a fine temporal scale could elucidate population structure of gadoids. We focus on three species (saithe, pollack, and cod) where age readings were routinely conducted and analyse their dynamics in terms of abundance and growth. In particular, we hypothesize that cod in Masfjorden consists of two components, migratory bank cod and resident fjord cod, and that the presence of the migratory component is visible in the seasonal dynamics of growth and mortality. More precisely, the presence of migratory bank cod should be detectable based on reduced apparent mortality and increased mean size-at-age when the bank cod enter the fjord prior to spawning in winter, and based on increased apparent mortality and reduced mean size-at-age when they leave the fjord after spawning. When juvenile bank cod leave the fjord, apparent mortality should again increase, but we have no prior information about when this could happen, and whether this happens in a synchronized manner at all. We first analyse the material using annual aggregation, which is the temporal resolution typically available for multiannual studies. We contrast this with seasonal analyses, an opportunity seldom available in studies spanning several years.

Material and methods

The data were collected in a monthly experimental fishery in the Masfjorden area (60°50'N 5°25'E) from October 1985 to June 1993. Masfjorden is a 22-km long, typical fjord in western Norway with maximum depth of 500 m, sill depth of 75 m, surrounded by steep mountains, with mainly steep and rocky sides and some shallow bays, and with more shallow areas just outside the sill (Salvanes and Nordeide, 1993). Based on the original sampling design, the observational unit of the experimental fishery in Masfjorden is a "net group". Each net group consisted of two trammelnets (45- and 70-mm stretched mesh in the inner net for the two nets, respectively, and 261-mm stretched mesh in the outer nets of both trammelnets) and one gillnet (39-mm stretched mesh) situated within 30 m of the shore. The net groups fished during an approximately 15-h period including night, at shallow depths of approximately 5–20 m. Approximately 40 nets were set each month (with a few exceptions) at random locations within the fjord, after excluding topographically unfavourable locations.

The available database does not allow consistently identifying which nets constituted a net group, and we had to treat a net soaked overnight as the sampling unit. Similarly, there was some sampling outside the target depth range (5–20 m), mostly with only one of the standard gillnets. We excluded all nets where the shallower end was deeper than 20 m. This resulted in a sampling effort of 3218 nets, distributed by year and quarter, as in Table 1, with all gillnet types used with almost the same frequency.

To be able to utilize the samples from the deeper part (>20 m) of the fjord, we created an additional dataset based on the smaller-meshed trammelnet only (45-mm stretched mesh in the inner net), the net most frequently used in deeper waters. This net was used 1122 times in shallow waters (included in the main dataset; Table 1), and 220 times in deeper waters (the depth of the shallower end in 21–58 m depth), evenly spread throughout the seasons.

The fish were kept on ice until examined the same day for total length (nearest cm), weight (nearest g), and stage of maturity (1, "immature"; 2, "maturing"; 3, "spawning"; 4,

"spawned/resting"; 5, "uncertain") by visual inspection of the gonads (Fotland *et al.*, 1995). Otoliths were removed and later analysed; all ages are expressed relative to 1 January as the nominal date of birth. More details about the Masfjorden area, gears, sampling, data collection and gear selectivity are found in Salvanes (1991) and Salvanes and Nordeide (1993).

The net groups caught cod larger than 17–18 cm (age 1 and older) non-selectively with respect to length (Salvanes, 1991). Selectivity for pollack and saithe has not been analysed, but because these species have similar body shape and size to cod, we assume here that the sampling can be considered as non-selective for these species also; Salvanes (1995) assumed so for pollack. The cod catches also contained released cultured cod (Smedstad *et al.*, 1994); only wild cod (identified as cod without a tag) were used in the analyses here.

For the annual analyses, we use data from years that were fully covered by the sampling programme (1986–1992). Sampling was monthly, but some months are missing, and sample sizes at monthly time-scale are low; therefore, we analyse the data at seasonal (quarterly) resolution. For the sake of simplicity, quarters 1–4 are referred to as "winter", "spring", "summer", and "autumn", respectively. For the quarterly analyses, we use all data from October 1985 to June 1993. Only net groups set within the fjord (Fosså *et al.*, 1994; Smedstad *et al.*, 1994) were used. The data selection is similar to earlier studies (Salvanes and Ulltang, 1992; Salvanes, 1995), but extends farther in time until the termination of the sampling programme.

Instantaneous total mortality rate (Z, year^{-1}) is estimated as $-\log(\mathrm{cpue}_{c,i+\Delta t}/\mathrm{cpue}_{c,i})/\Delta t$, where $\mathrm{cpue}_{c,i}$ is catch per unit effort, or simply catch rate, of cohort c at age i, and Δt is the time interval in years, here either 1 year or 3 months. Because changes in catch rate also reflect processes other than mortality, the estimate could be termed as "apparent mortality rate", but in the text we use "mortality rate" to simplify the presentation.

Growth was estimated as either increments in a cohort's mean length at consecutive time periods, or with the von Bertalanffy growth model estimated with non-linear least squares regression. Because differences in growth were marginal, sexes were combined. As for mortality, these methods only estimate "apparent growth", as changes in mean size are also influenced by processes other than growth.

Catch rates and length were modelled using generalized linear mixed models (GLMM), with Poisson (catch rate) or normal errors (length) and logarithmic link function. Quarter was treated as a factor and age as either a factor (catch rate) or a variate (length, log-transformed). Cohort and net were random effects. Because the effect of age alone is trivial (it merely shows that fish die, and grow when age increases), model with age alone was taken as the null model. Model selection was based on likelihood ratio tests and the Akaike Information Criterion (AIC); the outcome was independent from the approach. When depth was used as an additional variable to explain catch rates, we followed similar model selection procedure as described above. As the null model, we took model that best explained catch rates in this alternative dataset, without yet including depth as an explanatory variable. The model selection was then continued from this null model, with depth (a two-level factor) as an additional explanatory variable. All analyses were conducted in R (R Development Core Team, 2011) using package "lme4" for GLMM analyses (Bates *et al.*, 2011).

Results

Pollack is the most abundant of the three species studied in Masfjorden, followed by saithe and cod (Figure 1). Catches of all these species are dominated by young fish, with relatively few individuals older than ages 3–4 caught. No saithe older than age 5 were caught, whereas pollack and cod up to ages 8–10 were occasionally captured (one pollack was aged to 13 years). Saithe in Masfjorden were almost entirely immature. In contrast, for pollack and cod, significant proportions of mature fish were caught.

Catch curves show that the studied species were fully recruited to the experimental fishery at age 1 for pollack and age 2 for saithe and cod (Figure 2). For pollack and cod, total mortality Z appears constant at ~1.0 year^{-1} after full recruitment. For saithe, mortality increases with age; from age 2 onwards, Z is >1.0 year^{-1}. All species show growth that, as expected, slows down with age (Figure 3). Growth is similar for male and female fish for all three species. Asymptotic length from the von Bertalanffy growth model is within the species-typical range (Cohen *et al.*, 1990; Muus and Nielsen, 1999; Froese and Pauly, 2011) for pollack and cod, but is very low for saithe. Similarly, maximum length of saithe (84 cm) is low for the species, whereas values for pollack (87 cm) and cod (107 cm) are normal.

The virtual lack of large, old, mature saithe, and the very high mortality estimated for the oldest age groups encountered in Masfjorden, suggests that saithe may migrate out from the fjord once they reach maturity (no tagging data exist to confirm this proposition). In contrast, large and old pollack and cod are present in appreciable numbers in the fjord, and they show practically constant mortality from recruitment to old age. The proportion of mature cod and pollack is not very high even in the older age groups, but this could result from misclassifying "resting" mature fish as immature outside the spawning season. Thus, the annual data suggest that pollack and cod in Masfjorden can parsimoniously be considered as closed populations.

At a finer time-scale, abundance does not decline smoothly with age for any of the studied species (Figure 4), but instead shows seasonal, age-dependent patterns that are statistically significant (Table 2). For saithe, catch-at-age tends to decline throughout the year, except between the third and the fourth quarters when it increases; correspondingly, the estimates of mortality are negative. For cod, catch rate declines most of the time, and mortality estimates do not show striking patterns (apart from one outlier caused by low catch rate at age 4 in the third quarter). For pollack, seasonal catch rate fluctuations are very pronounced. During the first half of the year, catch rate-at-age increases in the majority of cases, whereas during the second half of the year, catch rate always declines and mortality estimates are consistently very high ($Z \geq 2$ year^{-1}).

The spread of the mortality estimates is the smallest for cod, whereas especially for pollack, there are many very high and very low estimates ($|Z| > 2$ year^{-1}). The seasonal fluctuations in the apparent mortality are somewhat similar between cod and saithe, whereas pollack shows fluctuations in the opposite phase.

To elucidate the possible role of seasonal changes in depth distribution, we tested whether depth influences catch rates of the trammelnet that was most often used outside the main sampling depth. Catch rates were significantly lower in the deep nets for cod, but the

effect was independent of the season (Table 3). For saithe and pollack, the effect of depth was strongly season-dependent, but in the opposite ways. For pollack, catch rates in the deep are much reduced in summer compared to the shallow nets, whereas for the rest of the year, deep nets are relatively more effective. For saithe, the opposite is true: deeper nets are relatively more effective in summer, whereas shallower nets are more effective at other times.

Length increases relatively smoothly with age, and mostly throughout the year, for all three species (Figure 5); age- and season-specific fluctuations in growth are statistically significant for all species (Table 2). For saithe, growth is fast until age 2, and then slows down and becomes poorly estimated when relatively few saithe are left in Masfjorden. For pollack, growth is fastest during summer and autumn, but continues throughout the year except for older ages where samples sizes become low. For cod, the growth pattern shows complex seasonal changes. Quite unexpectedly, mean size shows a marked increase during summer for age 1 cod only, whereas for older cod, changes in mean size are negligible at the time when the other two species show their fastest growth. For rest of the year, growth estimates are positive with just one exception; consistently high growth is observed in autumn.

Changes in depth distribution do not explain variations in mean length. The trammelnets in deep waters caught significantly larger saithe (on average 9.0% larger, likelihood ratio test: $p < 0.001$) and pollack (2.0% larger, $p = 0.033$), but not cod ($p = 0.114$), than those in the main sampling depths. For none of the species did the effect of depth vary with season ($p \geq 0.076$).

In Figure 6, growth and maturation dynamics are overlaid for pollack and cod. Maturing pollack are observed in significant numbers during all seasons except in late summer (third quarter), and spawning pollack mostly in spring (second quarter). Immature pollack are present in high numbers until age 4, suggesting that distinguishing juvenile and resting adult pollack may be difficult. Compared to pollack, the spawning season of cod occurs earlier, with spawning fish observed almost solely in winter (first quarter). The growth curve of cod is much less smooth than that of pollack, and shows consistently higher variability in length-at-age. The conspicuous feature of the cod growth curve is that after age 1, average length is essentially unchanged in summer, whereas growth occurs during other seasons (as seen also in Figure 5).

Discussion

Inspecting seasonal data for saithe, pollack, and cod in Masfjorden reveals very rich dynamics. Seasonal fluctuations in abundance, and to a lesser extent in length, are marked for all species. These seasonal patterns could reflect seasonal changes in mortality and growth. However, the general limitation of the analyses presented in this paper is that we cannot disentangle changes that are caused by the fundamental population processes of growth and mortality and those caused by seasonal and size-dependent variations in catchability and availability. Below, we discuss the interpretation of our findings against what is known about population ecology and structure of the three species and the possible confounding effects of variable catchability and availability.

Our results are in agreement with what is generally known about the life history of saithe along the west coast of Norway (Nedreaas, 1987; Smedstad, 2008), but no information has previously been published in the primary literature. Adult saithe can undertake very long migrations (Jakobsen and Olsen, 1987). It is believed that the North Sea saithe stock spawns near Shetland, and that the west coast of Norway is an important nursery area. According to Smedstad (2008), saithe migrate away from the coast during spring at ages 3–4, whereas Nedreaas (1987) reported migration already at age 2, with an indication that large fish migrate first. Bergstad (1991) found 3- and 4-year-old saithe to dominate catches in the deeper waters off the coast, suggesting a gradual migration from inshore to offshore. According to Smedstad (2008), saithe mature at ages 4–6 at a length of about 50 cm; this length is similar to the asymptotic length of saithe in Masfjorden. No saithe older than 5 years was encountered. Our results from Masfjorden thus conform to the earlier information on the saithe life cycle, and Masfjorden appears to be predominantly a nursery habitat for saithe. However, some mature (but not spawning), larger saithe are present in Masfjorden, showing that individual variation in the migration pattern exists.

Population ecology of pollack is little known, both along the coast of Norway and in general (ICES, 2011a). The maximum age recorded in Masfjorden (13 years) is well above the maximum age given in reference works (Cohen *et al.*, 1990; Froese and Pauly, 2011), perhaps based on Moreau (1964). However, both Pethon (1998) and ICES (2011a) suggest a maximum age of 15 years or more, without citing specific sources.

Population structure of pollack remains little studied too. Landings data show two fairly distinct centres of distribution, one in the northern North Sea/Skagerrak extending north along the Norwegian coast, and one between the English Channel, the Irish Sea, and the northern part of the French west coast (ICES, 2011a). However, a study by Charrier *et al.* (2006) found no evidence of significant genetic differentiation between a sample from southern Norway and samples from the English Channel. A single tagging experiment along the Norwegian west coast resulted in mostly local recaptures, leading Jakobsen (1985) to suggest that pollack along the Norwegian coast may consist of local stocks separate from North Sea pollack. Fromentin *et al.* (1998) have shown that in the inshore habitats, dynamics of 0-group pollack are spatially correlated, possibly reflecting shared, large-scale environmental drivers. Spawning of pollack is said to occur offshore (Muus and Nielsen, 1999). While we have no direct observation of spawning, pollack considered to be in the spawning stage based on macroscopic inspection of gonads were common during the second quarter (Figure 6). While we cannot exclude the possibility that pollack migrate out of Masfjorden for spawning, perhaps even to the open sea (about 40 km away from the mouth of the fjord), the most parsimonious interpretation is that spawning occurs locally. Thus, our results suggest that pollack in Masfjorden function as a dynamically independent unit and can be considered as a self-renewing substock. This interpretation is in agreement with the tagging study by Jakobsen (1985). Salvanes (1995) also suggested that migration is not significant for pollack in Masfjorden, without commenting whether spawning occurs locally.

Of the studied species, population ecology of cod in Masfjorden remains the most enigmatic. Based on tagging studies (Salvanes and Ulltang, 1992) and anecdotal evidence, we

hypothesized that cod in Masfjorden could represent resident (fjord cod) and migratory (bank cod) components, the latter being present in the fjord for the spawning season only. There are patterns that are compatible with seasonal mixing of bank and fjord stock components, namely the high variability in length-at-age (Figure 6) and the peculiar seasonal growth pattern (Figure 5; see discussion further below), but the evidence remains very ambiguous; it remains possible that the signal was lost in noise because of small sample sizes (cf. Table 1). Do all cod in Masfjorden represent a single stock component? While early genetic studies could not refute this hypothesis (Jørstad *et al.*, 1994), the methods of those times lacked power to detect differences. Therefore, we suggest that the hypothesis of two stock components should not yet be rejected, but that the hypothesis needs a refinement. Thus, we suggest that the putative fjord cod in Masfjorden have a wider range than only Masfjorden, i.e. extending to the adjacent fjords. While juvenile cod in Masfjorden are considered stationary (Salvanes and Ulltang, 1992), this may not apply to mature cod. Indeed, Salvanes and Ulltang (1992) found that a few cod tagged in Masfjorden during summer were recaptured outside the fjord. If both fjord and bank cod are migratory, albeit to a different degree, it becomes very difficult to detect the signatures of emigration and immigration in abundance and size data. Furthermore, the sampling in Masfjorden was designed to capture local cod, and it is possible that it was less than ideal for larger, migratory cod.

The most surprising feature is that cod, apart from fish up to age 1, appear to grow least during summer and most in autumn. This finding has at least four possible explanations that are not mutually exclusive:

- Fishing, both recreational and commercial, is positively size-selective and disproportionally removes the largest, fast-growing fish within an age class (Kristiansen and Svåsand, 1998). For this mechanism to explain lack of growth in summer, fishing activity would need to be highest at that time. However, this explanation alone appears insufficient for younger age classes because Salvanes and Ulltang (1992) estimated fishing mortality to be moderate at $F = 0.14–0.28$ year^{-1} for ages 2–3, and relatively high only for age 4 and older ($F = 0.64$ year^{-1}).
- Size-dependent changes in depth distribution and the resulting changes in availability of fish to the survey gear could explain growth anomalies: if large cod show the highest tendency to move to deeper waters in summer, an apparent lack of growth in summer, followed by a growth burst in autumn, would ensue. However, we found no evidence for deeper distribution of cod in summer (Table 3).
- Warmer temperature in summer could lead to reduced activity in cod, and more so in larger individuals, which will generally have more difficulty in satisfying their respiratory needs when temperature increases (Pauly, 2010). Because gillnets are passive gear, lower activity would lead to lower catch rate (Hamley, 1980), and if the temperature effect is significantly size-dependent, would negatively bias mean size.
- Mixing of population components could cause the observed anomalies in length-at-age. We expect that if migratory coastal cod were to enter Masfjorden for spawning, they would cause a positive anomaly in length-at-age because cod in Masfjorden are slower-growing than those along the coast. Indeed, the period of the highest increase in average

length coincides with the period of lowest apparent mortality, which could be caused by immigration. However, when the presumed migratory cod leave Masfjorden after spawning, apparent mortality should increase and growth decrease. Notwithstanding that the data are noisy, there is no such increase in mortality, whereas the growth decline occurs late relative to the spawning season; a possibility is that the latter is caused by large juvenile cod leaving the fjord. We also note that variability in length-at-age, while consistently higher for cod compared to pollack (Figure 6), is not higher during the spawning season compared to the rest of the year. Thus, this explanation is not sufficient to explain the patterns in length-at-age.

At present, we can only conclude that size-selective fishing, reduced activity, and migration could all be contributing to the apparent summer growth stanza in cod. However, studies of archived otoliths could help to resolve this puzzle, and the one about the population structure: growth back-calculations would help to decide whether the growth pattern suggested by our results is real, and genetic analyses (Therkildsen *et al.*, 2010) might help to reveal whether cod in Masfjorden represent one or more population components—modern genetic tools offer better resolution than those available to Jørstad *et al.* (1994). Indeed, genetic methods have helped to detect mixing of multiple stock components for cod elsewhere (Wennevik *et al.*, 2008; Kovach *et al.*, 2010).

All studied species displayed marked seasonal patterns in age-specific catch rates. These were least pronounced for cod, with the most prominent pattern being low mortality in autumn. The potential reasons for this have been discussed above; seasonal changes in depth distribution seem not to be important for cod. For saithe and pollack, the seasonal fluctuations are very pronounced. For saithe, the catch rates plummet in spring, which is the season when saithe are believed to migrate away from the coast (Nedreaas, 1987; Smedstad, 2008). For pollack, the patterns are almost the opposite of saithe: catch rates of pollack plummet in autumn. Our results show that migrations between deeper and shallower waters are contributing to these patterns (Table 3). The contrasting patterns might be related to different thermal preferences: pollack is a more southern species than saithe (Cohen *et al.*, 1990; Pethon, 1998; Froese and Pauly, 2011), and it is conceivable that it seeks warmer surface waters in summer while avoiding cold surface water in winter. The opposite could be true for saithe, although avoiding interspecific competition might also contribute to the contrasting depth distributions. An alternative explanation is that saithe has more pelagic distribution in summer. Unfortunately, we have no data to further evaluate these hypotheses.

Total mortality rates are high for all studied species, even for larger individuals that are relatively safe from natural predation: in the absence of large predatory fish, piscivory must be negligible for gadoids larger than about 30 cm in length (Kristiansen *et al.*, 2000). For saithe, the high mortality is likely an artifact: both earlier information and observations from Masfjorden suggest that the high (apparent) mortality rates are caused by emigration. All species are taken in recreational and small-scale commercial fisheries, and for cod and pollack, fishing has been shown to be an important source of mortality (Salvanes and Ulltang, 1992; Salvanes, 1995). While the asymptotic and maximum sizes of pollack and cod are not abnormal, they are at the low end of the typical range, which further suggests that fishing is

contributing to high total mortality rates (Kristiansen and Svåsand, 1998; Kristiansen *et al.*, 2000).

The practical implication of our results is that the strong seasonal patterns in age-specific catch rates will cause fish abundance estimation to be very sensitive to timing of surveys. Practical constraints often result in changes in timing of surveying. However, because seasonal climatic patterns are not constant either, even surveys conducted at the same calendar dates may also encounter unexpected differences in catch rates that are unrelated to "real" changes in abundance. Similarly, a study not covering a whole year may give very biased estimates of mortality and growth.

Analysis of seasonal abundance and size data has revealed very high dynamism in cod, pollack, and saithe in Masfjorden, and marked differences between the species. These differences originate from differences in population structure and in seasonal migrations, influencing their catchability and availability to survey gears. Our study highlights the importance of accounting for seasonal variability when studying the dynamics of fish stocks, and helps to understand population ecology of these ecologically and economically important species.

Supplementary material

The following supplementary material is available at the ICESJMS online version of the manuscript: Figure S1, which is similar to Figure 6 in the main text, but including individuals with "uncertain" maturity stage.

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Table 1. Overview of the study material. Sampling effort is the total number of nets soaked overnight. For saithe, pollack, and cod, total sample sizes for each year and quarter are given. In total, there were 3546 saithe, 5322 pollack, and 1708 cod with a known age.

	Quarter	Year								
		1985	1986	1987	1988	1989	1990	1991	1992	1993
Effort	1		89	112	114	117	112	106	114	107
	2		89	105	114	86	70	85	109	108
	3		111	116	109	116	115	116	111	
	4	96	119	160	116	90	68	73	65	
Saithe	1		92	90	58	237	161	116	135	196
	2		148	74	85	72	32	12	47	78
	3		137	120	284	81	74	41	122	
	4	232	240	87	202	126	51	77	39	
Pollack	1		48	73	125	239	80	79	57	86
	2		195	34	309	231	54	180	203	123
	3		256	104	450	300	230	407	281	
	4	157	122	133	377	88	142	67	92	
Cod	1		76	57	128	107	55	25	25	28
	2		52	42	114	62	17	26	15	25
	3		62	61	155	39	33	20	12	
	4	87	82	129	107	42	15	6	4	

Table 2. Modelling the effects of age and quarter on catch rate (number of fish per net per night) and length (cm). Ages 1–5 (cod and pollack) and ages 1–4 (saithe) are used. See the methods for description of the generalized linear mixed models used.

	Saithe			Pollack			Cod		
Model	**Model d.f.**	**AIC**	***p***	**Model d.f.**	**AIC**	***p***	**Model d.f.**	**AIC**	***p***
Catch rate~age	6	7 890.0		7	11 223		7	5 594.9	
Catch rate~age+quarter	9	7 753.4	<0.001	10	10 932	<0.001	10	5 533.9	<0.001
Catch rate~age×quarter	18	7 633.9	<0.001	22	10 804	<0.001	22	5 529.2	0.004
Length~age	5	12 706		5	20 176		5	12 180	
Length~age+quarter	8	12 245	<0.001	8	18 860	<0.001	8	11 956	<0.001
Length~qge×quarter	11	11 283	<0.001	11	16 499	<0.001	11	11 527	<0.001

Table 3. Modelling the effect of sampling depth on catch rate (number of fish per net per night). Data from all depths, but only one net type are used. Ages 1–5 (cod and pollack) and ages 1–4 (saithe) are used. "NM" represents a null model including the main effects of age and quarter (all species) and their interaction (saithe and pollack). The lower part gives parameter estimates for the best models. Depth is a binary factor, with the shallow samples as the reference level. "Effect" describes the multiplicative effect that depth has on catch rates (=exponential of the parameter estimate).

	Saithe			Pollack			Cod		
Model	Model df	AIC	*p*	Model df	AIC	*p*	Model df	AIC	*p*
Catch rate~NM	18	3064.2		22	4158.3		10	2175.0	
Catch rate~NM+depth	19	3060.6	0.019	23	4159.3	0.318	11	2149.4	<0.0
Catch rate~NM+depth*quarter	22	3050.0	<0.001	26	4076.2	<0.001	14	2154.8	0.8
	Estimate	s.e.	Effect	Estimate	s.e.	Effect	Estimate	s.e.	Effe
Depth (quarter 3)	1.00	0.44	2.72	-1.96	0.28	0.14	-0.84	0.17	0.4
Depth, quarter 1 vs. 3	-2.41	0.63	0.09	2.98	0.35	19.7			
Depth, quarter 2 vs. 3	-2.00	0.69	0.13	2.31	0.34	10.1			
Depth, quarter 4 vs. 3	-1.76	0.73	0.17	1.73	0.36	5.63			

Figure legends

Figure 1. Catch rate (mean ±1 s.e.) per age group for saithe, pollack, and cod in Masfjorden in 1986–1992. Maturity proportions were calculated as simple means for all sampled individuals, excluding those with unknown or uncertain maturity stage. Note different vertical scale for pollack.

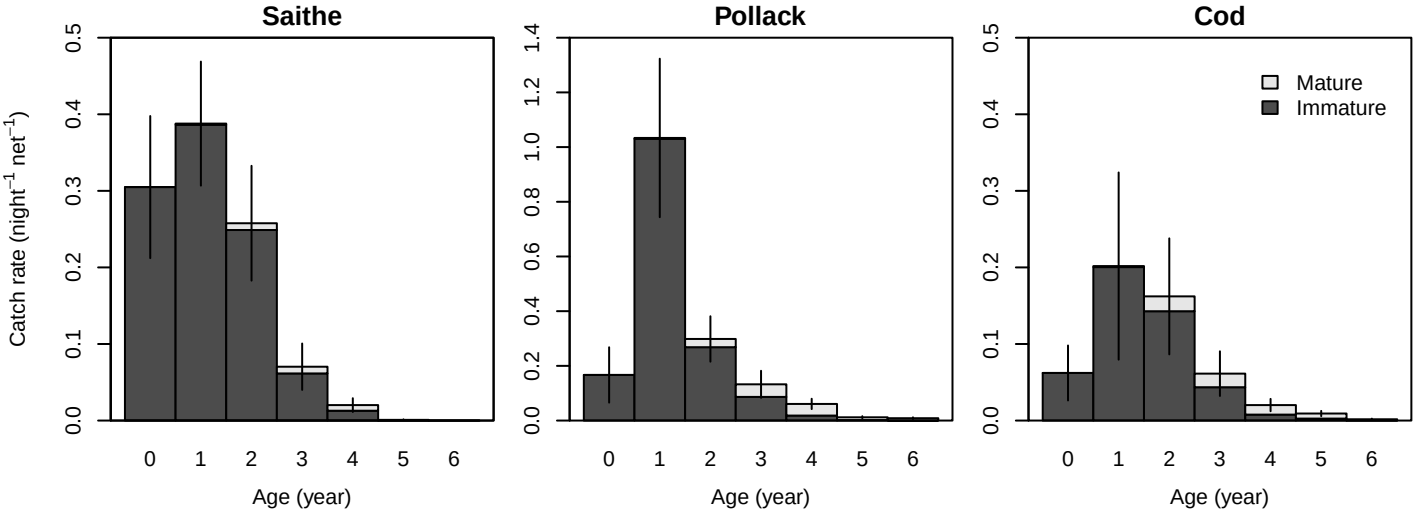
Figure 2. Catch curves for saithe, pollack and cod in Masfjorden. The data are the same as plotted in Figure 1. Grey dashed lines correspond to total mortality $Z = 1.0$ year^{-1} shown for reference.

Figure 3. Length at age for saithe, pollack, and cod in Masfjorden in 1986–1992. Age is expressed in full years except for the 0-group, which is assigned age 0.5, the age when the fish become available to the experimental fishery. Vertical bars correspond to ±1 s.d. Fits of the von Bertalanffy model are shown by the grey curves.

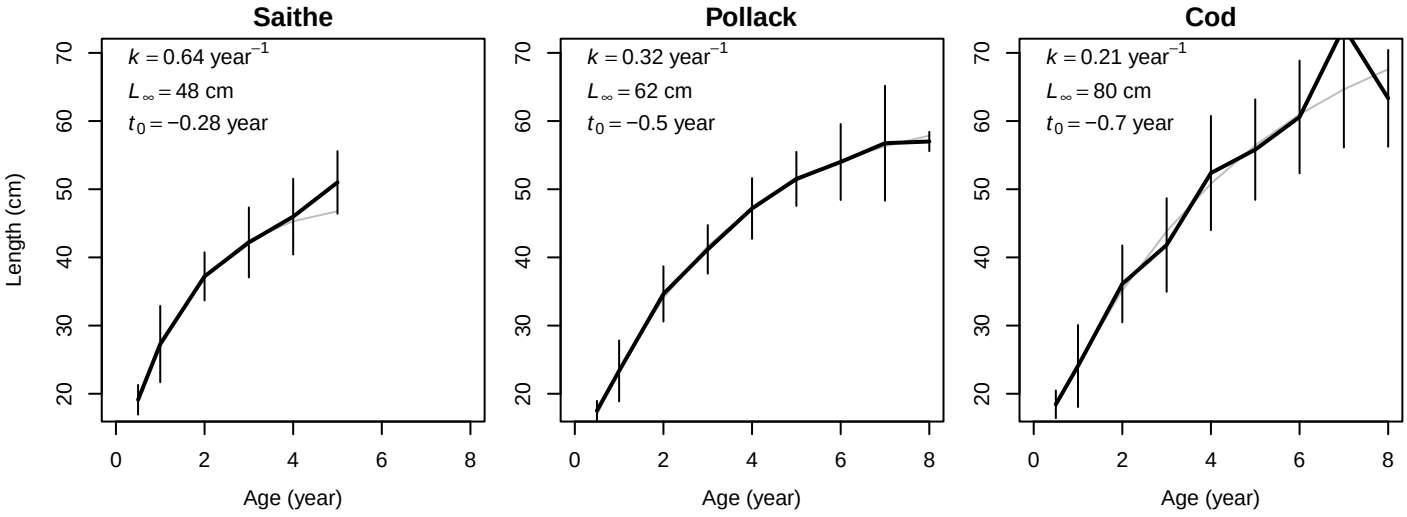
Figure 4. Quarter- and age-specific estimates of catch rate (top) and mortality (bottom) for saithe, pollack, and cod in Masfjorden in 1985–1993. Age in full years is shown by the black circles. Grey background corresponds to the colder half of a year (fourth–first quarters). Mortality estimates are aligned with the middle of the time intervals to which they apply. 0-group is omitted for clarity. Note the logarithmic scaling of the vertical axis in the top row.

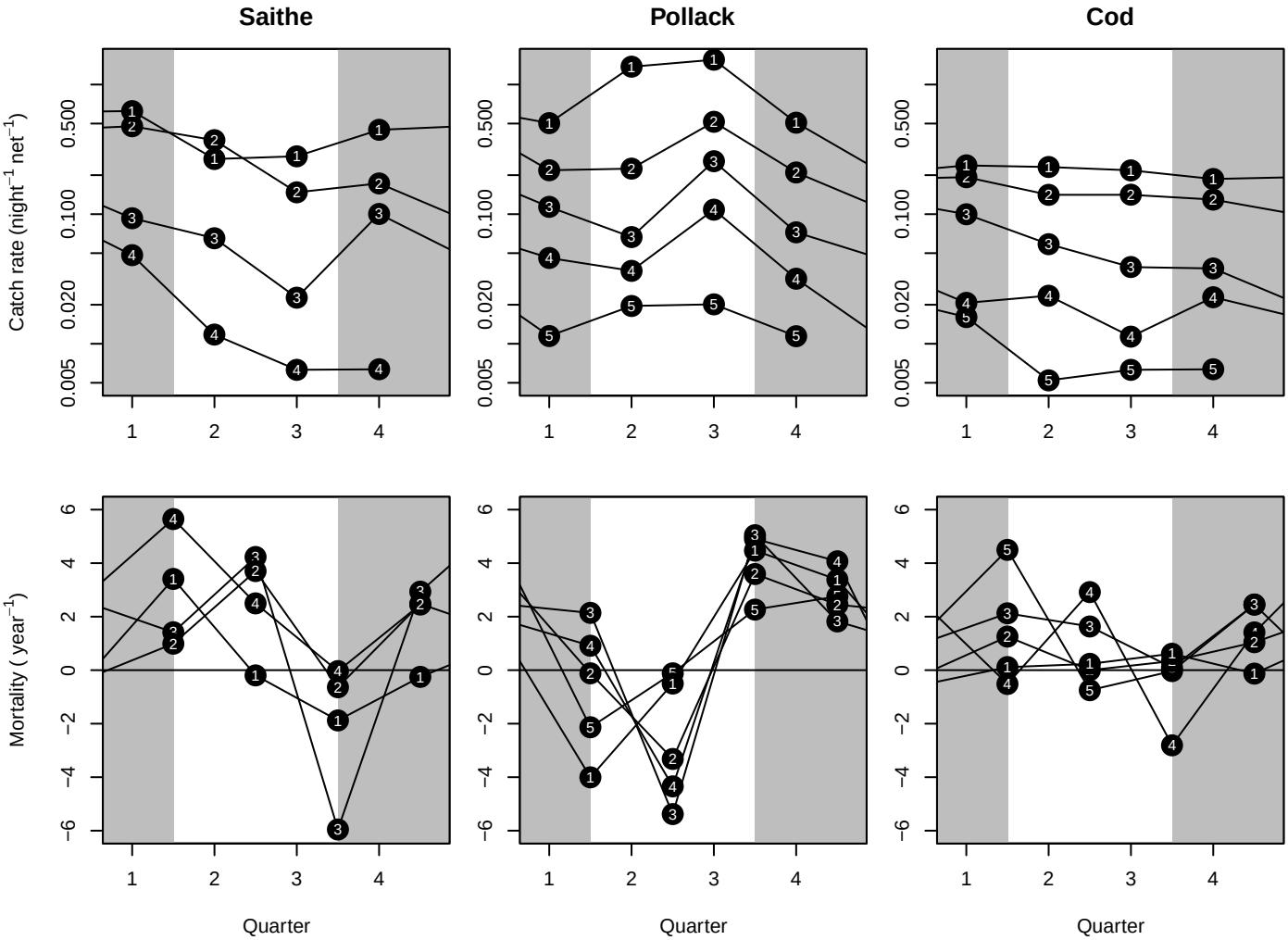
Figure 5. Quarter- and age-specific estimates of length (top) and growth (bottom) for saithe, pollack, and cod in Masfjorden in 1985–1993. Grey background corresponds to the colder half of a year (fourth–first quarters). Growth estimates are aligned with the middle of the time intervals to which they apply.

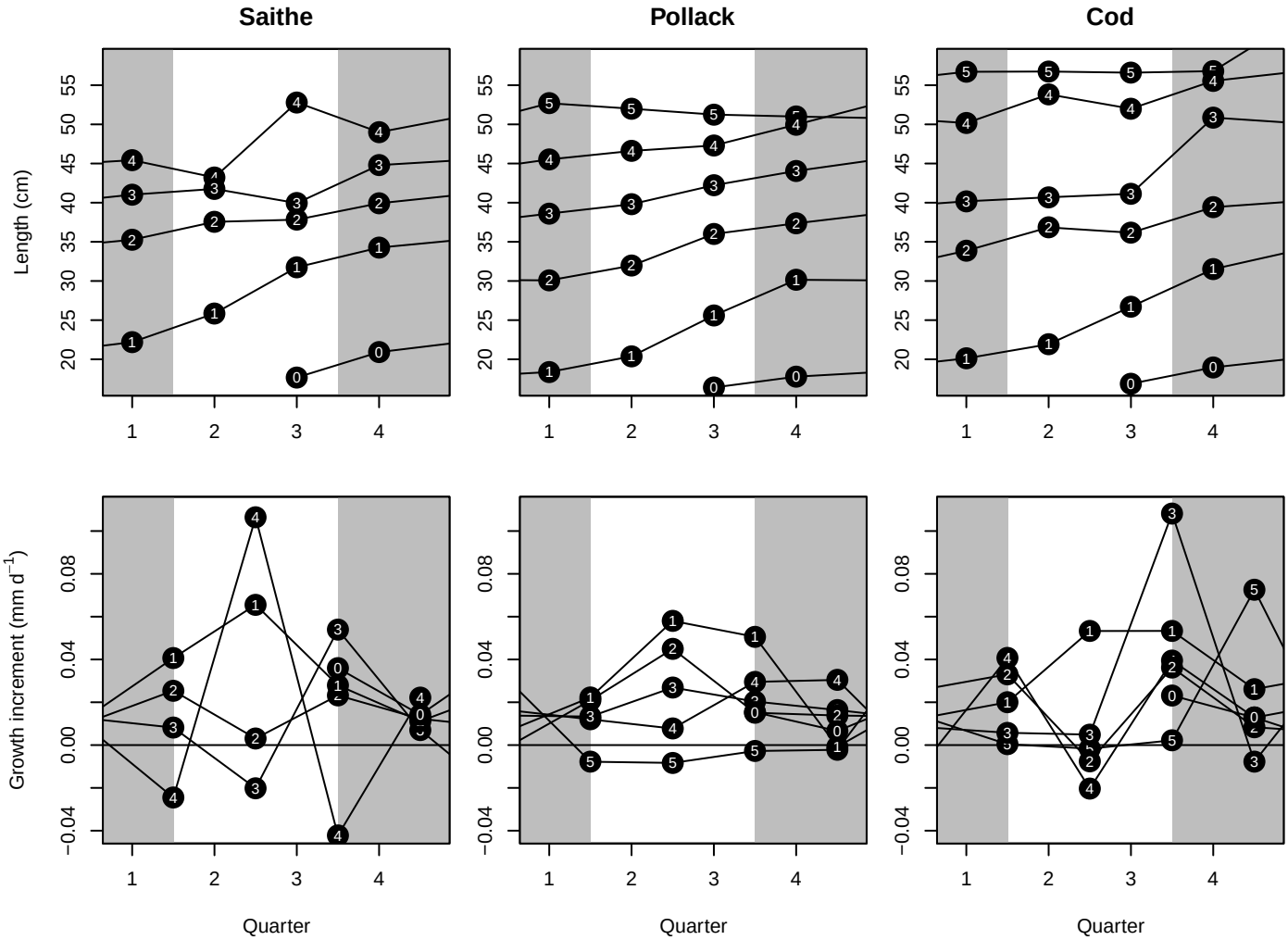
Figure 6. Growth and maturation dynamics of pollack and cod in Masfjorden. Abundance is shown per age and maturity stage. Circle radii are proportional to the logarithm of catch rate (number of fish per net per night). Maturity stages are numbered from one to four, corresponding to “immature”, “maturing”, “spawning” and “spawned/resting” stages, respectively. Growth curve, with the vertical bars showing ±1 s.d., is shown on the secondary vertical axis. Grey background corresponds to the colder half of a year (fourth–first quarters). Individuals with “uncertain” maturity stage are omitted here; see the Supplementary material Figure S1 for a version where these data are included.


Saithe
Pollack
Cod
Catch rate (night^{-1} net^{-1})
Age (year)
Mature
Immature
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.8
1.0
1.2
1.4
0
1
2
3
4
5
6

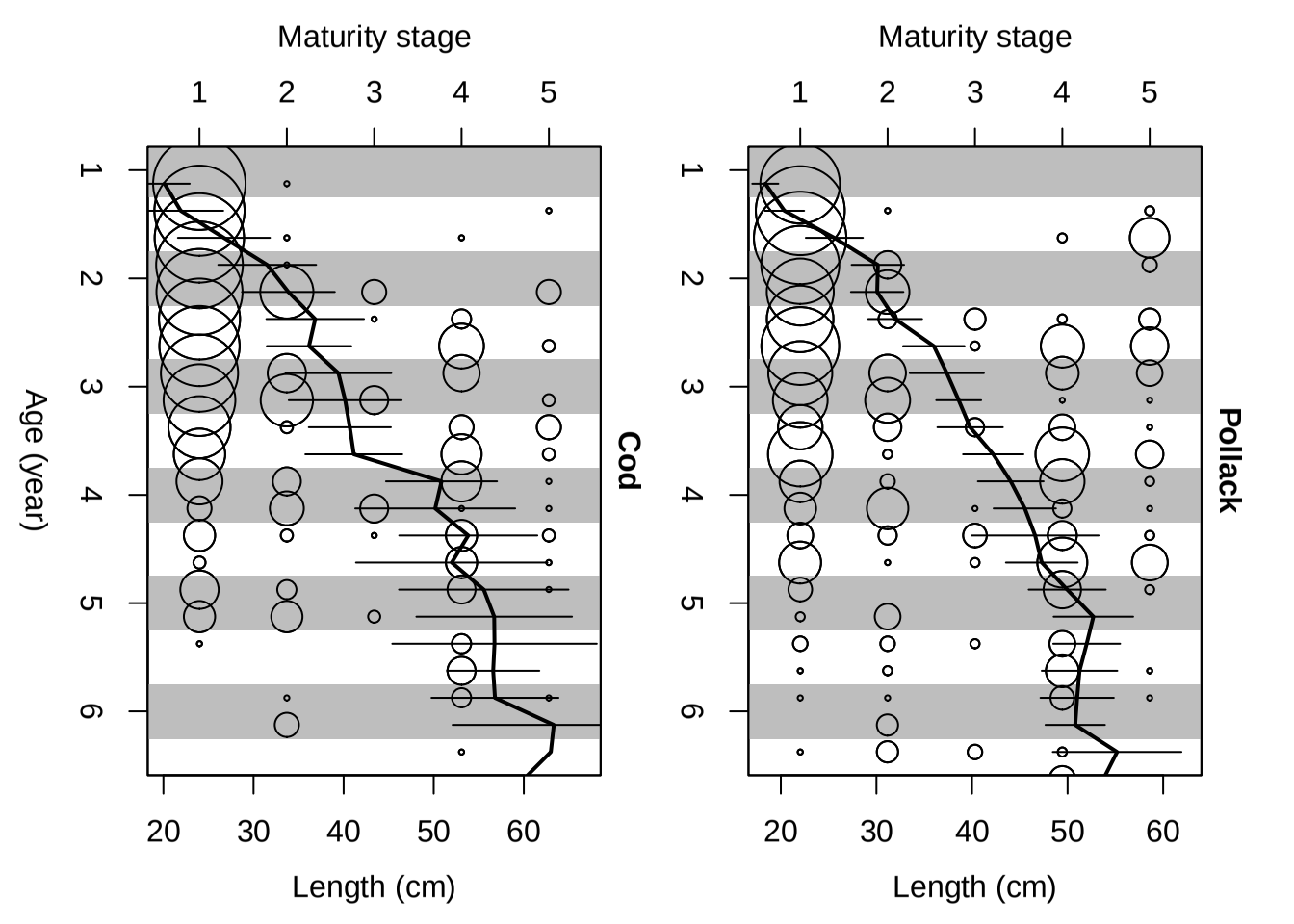
Saithe
Pollack
Cod
Catch rate (night^{-1} net^{-1})
0.500
0.050
0.005
0.001
0
2
4
6
8
Age (year)


Saithe
$k = 0.64$ year^{-1}
$L_\infty = 48$ cm
$t_0 = -0.28$ year
Pollack
$k = 0.32$ year^{-1}
$L_\infty = 62$ cm
$t_0 = -0.5$ year
Cod
$k = 0.21$ year^{-1}
$L_\infty = 80$ cm
$t_0 = -0.7$ year
Length (cm)
Age (year)
20
30
40
50
60
70
0
2
4
6
8


Saithe
Pollack
Cod
Catch rate (night^{-1} net^{-1})
0.005
0.020
0.100
0.500
Mortality (year^{-1})
−6
−4
−2
0
2
4
6
1
2
3
4
Quarter


Saithe
Pollack
Cod
Length (cm)
Growth increment (mm d^{-1})
Quarter
Quarter
Quarter

Pollack
Maturity stage
Length (cm)
1
2
3
4
20
40
60
Cod
Maturity stage
Length (cm)
Age (year)
1
2
3
4
5
6


Maturity stage
1
2
3
4
5
Age (year)
1
2
3
4
5
6
Cod
20
30
40
50
60
Length (cm)
Maturity stage
1
2
3
4
5
1
2
3
4
5
6
Pollack
20
30
40
50
60
Length (cm)